EAR PLUG LAMINATIONS IN RELATION TO THE AGE COMPOSITION OF A POPULATION OF FIN WHALES (BALAENOPTERA PHYSALUS)

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SYNOPSIS

1. The method of grinding the ear plugs of Fin Whales and of counting their laminae is briefly described.
2. The growth of the plug is compared with that of the skull width and body length.
3. A provisional rate of formation of the laminae is assessed and correlated with previously established data about the growth and age of Fin Whales.
4. From the age frequency distribution based on the ear plug lamination analyses the apparent natural mortality rate for the " Sanctuary " population is demonstrated.

In the course of a detailed description of the ear plug of the Mysticeti (Purves, 1955) it was suggested that there might be a correlation between the laminar structure of the core of the plug and the age of the animal from which it was taken. Further support was given to this hypothesis by the examination of 18 Fin Whales at Steinshamn, Norway, during the summer of 1955, when the age as estimated from the ear plugs was compared with that assessed from the ovaries and baleen plates, Laws & Purves (1956), Ruud (1945).

The results of this enquiry were sufficiently encouraging to warrant further investigation. Since the National Institute of Oceanography is concerned with age determinations, especially in studies of the life cycle and populations of whales, Dr. Mackintosh and Dr. Laws had made arrangements, after the publication of the paper by Purves (1955) for the collection of a large number of ear plugs from whales taken by factory ships in the Antarctic season of 1955–56. The plugs were obtained from some 454 whales, together with relevant data on the whales from which they were taken. Before examining the material themselves however, they were good enough to make the collection available to us so that the relation between the laminations of the plug and the age of the whales could be further examined. This is the subject of the greater part of the present paper. It was a matter of much interest however, to examine the age composition of the population from which the plugs were obtained and by agreement with the National Institute of Oceanography the paper has been extended beyond its initial scope to include this aspect.

MATERIAL AND METHOD

The ear plugs had been wrapped singly or in pairs and preserved in 5% formaldehyde on board the factory ships and were consequently hard and in good condition for examination in the laboratory. It is unfortunate that a number of plugs had become detached from their wrappings during transit as a result of which it has been impossible to determine the length and sex of the animals involved, but even these specimens have been useful in plotting the age frequency distribution.

Because of the asymmetry and extreme attenuation of the distal end of the core it was thought that bisection of the plug would result in loss or damage to the earliest formed part of the structure, so each specimen was carefully group down to the central plane by hand. The grinding was carried out by rubbing the plug with a rotary movement against waterproof abrasive cloth which had been cemented with rubber solution to a sheet of plate glass. Coarse and fine grades of abrasive were used and during the whole operation a stream of water was directed over the surface of the plate. It is appreciated that for routine examination of the plugs a mechanical grinding plate or stone would be preferable, but since the time expended on each plug using the more primitive method amounted to no more than three minutes, the above described apparatus was considered adequate for the present sample.

Plate 5 shows a series of ear plugs from female Fin Whales, the specimens being chosen at random from groups of plugs which differed consecutively in lamination number by four laminations. The series shows a progressive lengthening of the core of the plug and a gradual darkening of its matrix from the external shell towards the central axis. From the plate it appears that the overall length of the core of the plug is no guide to the number of laminations which it contains, but it will be shown later that in spite of the great variability in the lengths of the cores of equal laminar number, the average length of the core per lamination number is correlated with the number of laminations. It may be stated that on the whole, the diminution in the thickness of the laminations from the distal to the proximal end of the core is more regular in plugs from males than in those from females. This characteristic is not always apparent in a small sample, and cannot be used as a guide to the sex of a whale from which any one plug originated but may be of use statistically in connection with a large sample of specimens. The unwrapped specimens referred to on page 161 were divided on the basis of this feature but the information so obtained has been of limited use and is referred to with reservation in the present paper.

In the plugs from immature and very young animals the primary laminations may be subdivided into a number of ill-defined, subsidiary layers but the latter become obliterated as more primary laminae are formed and it has been the practice throughout this investigation to treat every lamination in the older specimens as a single unit, however narrow and apparently subsidiary   In the very old specimens the proximal end of the core may appear to the naked eye or with dissecting binoculars to be quite undifferentiated, but when examined microscopically, these undifferentiated areas are seen to be made up of a series of regularly-spaced refractive layers. When these layers are counted towards the distal end of the core they are observed to increase gradually in thickness and in the latter respect to be in geometrically

progressive sequence with the coarser layers which are visible to the naked eye. The microscopic section shown in Plate 6 was taken from the proximal end of the only plug in which for some unknown reason there was a sharp transition from very coarse to very fine laminae, but it is useful in that a comparison can be made between the two types of laminae within the compass of a very small section. The section shows the appearance of the refractive layers referred to above after removal of the ceruminous component. The area bottom left, which shows the lateral extremity of the short axis of the base of the core originally contained very little cerumen and consists of a mass of undifferentiated squamae of keratin. On the right, the squamae are broken into a series of laminae of approximately equal thickness, each of which contains a number of flattened nuclei.

The upper part of the section shows two of the very coarse laminae. When stained with haemalum and Mallory's triple stain the greater part of the keratinized mass appeared bright blue, but in each lamina there was a conspicuous band of orange which occupied a position immediately distal to the layer of flattened nuclei. These bands of orange, which are deemed to mark areas of imperfectly keratinized cellular matter accompanying degenerate nuclei, seem to be the main distinguishing feature of the laminations and each can be used as a criterion of what is a single lamination. If it were possible to cut and stain the whole core in this manner the lamination number could be estimated with great accuracy. In the more simple method of counting the laminations on the unstained cut surface of the core it would be improbable to make an error of more than plus or minus 4 laminae in each plug and with a large sample, such as the one under consideration, errors of this magnitude would probably cancel each other out.

All the specimens referred to in this paper were collected aboard the factory ships *Baleana*, *Southern Harvester* and *Southern Venturer*. The *Southern Harvester* collection was obtained from that sector of the Antarctic known as the " Sanctuary " (Lat. 60° W.–120° W.) and is referred to as the Area I sample. The *Balaena* collection was obtained from Area II whilst the *Southern Venturer* collection was obtained from both sectors. The latter collection has been broken up and amalgamated with the *Balaena* and *Southern Harvester* specimens so that only the two populations, the Area I and Area II samples are described.

The data referred to in the text are given in Tables A to D of the Appendix.

From the results of the examination of the Steinsham material (*loc. cit.*) it has been established that there is a direct correlation between the number of laminations in the core of the plug and the age of the animal as assessed from the ridges on the baleen plates. This correlation can however be shown only in respect of animals under 6 years of age, since the analysis of the baleen plate data becomes difficult after this age.

Before attempting to obtain the age frequency distribution it is necessary to establish whether or not this age lamination correlation continues throughout life. It may reasonably be assumed that the growth of cetaceans follows a pattern similar to that which is found in most other mammals and that there is an age shortly after sexual maturity beyond which further increases in bodily proportions are small relative to the immature growth increments. This being so, one might expect a

certain variability in the adult dimensions due to the differential immature growth rates. If a simple relationship can be shown between the skull width and the lamination number as suggested by Purves (1955) then the lamination number would be valueless as a means of estimating the individual ages of a variable adult population the individual growth rates of which are unknown.

Unfortunately no data relevant to skull width are available for the present sample so that the skull-width-lamination number relationship cannot be found directly. Mackintosh & Wheeler (1929) have published a very comprehensive list of skull widths and body lengths of Fin Whales so we may use their figures relevant to the range of lengths available in the present sample to find the body-length skull-width relationship.

The Body Length, Skull-width Relationship

In the Tables of the External Characters of Fin Whales, Mackintosh & Wheeler (1929) quote the skull widths and total lengths of 162 female and 206 male Fin Whales taken at South Georgia during the years 1926 and 1927. The hypothesis
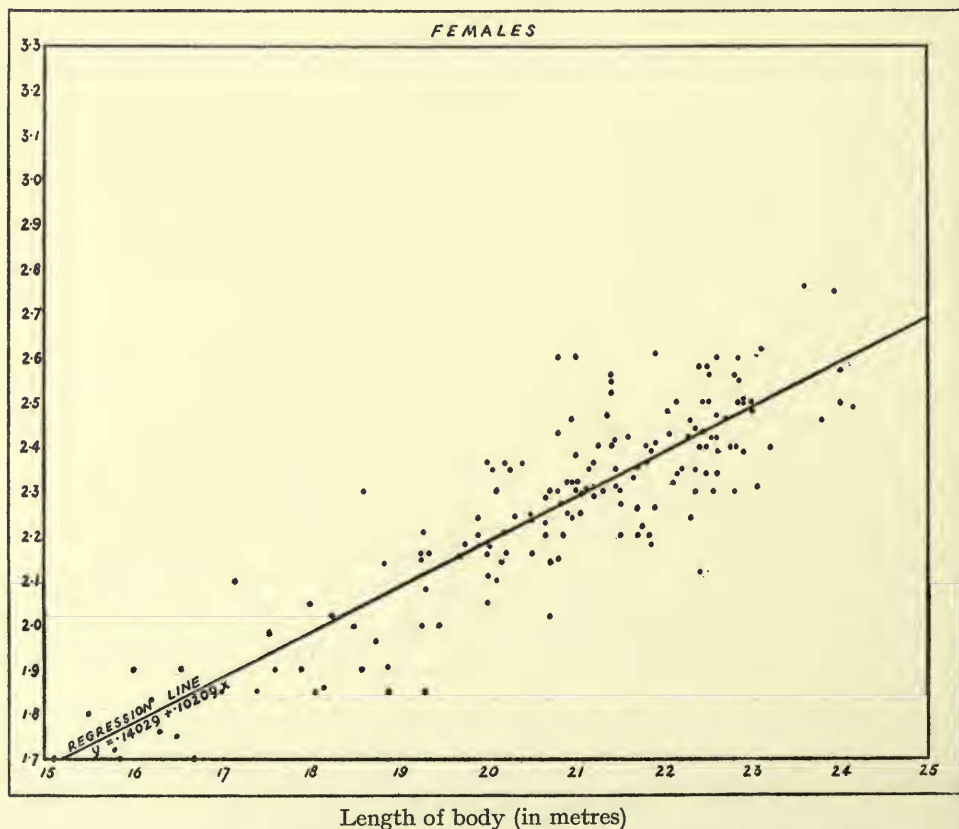

Length of body (in metres)

FIG. 1. The skull width-body length relationship of a population of female Fin Whales *Balaenoptera physalus* measured at South Georgia, Mackintosh & Wheeler (1926–27).

of a linear relationship between the skull-width and total length provides an excellent fit to the data. The linear regression of skull width on total length (Text-figs. 1 and 2) is found to be :

$y = 0.14029 + 0.10209x$ for females (Text-fig. 1) and $y = 0.02946 + 0.10813x$ for males (Text-fig. 2) where y and x are the skull width and total length in metres

Length of body (in metres)
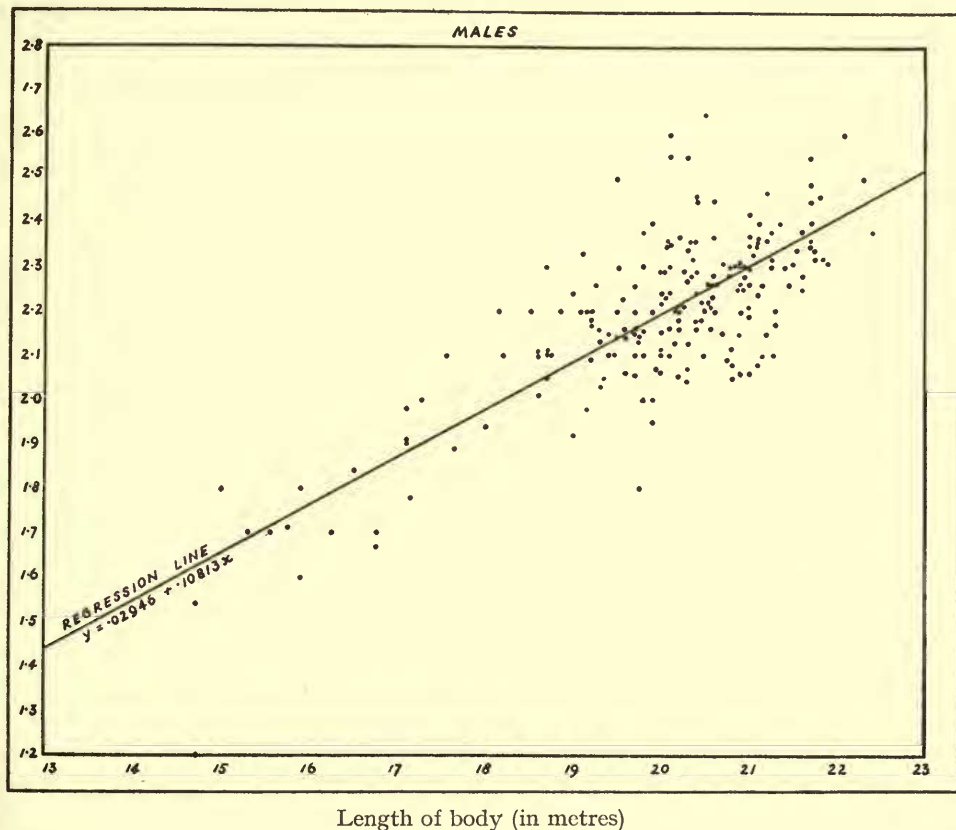
FIG. 2. The skull width-body length relationship of a population of male Fin Whales *Balaenoptera physalus* measured at South Georgia, Mackintosh & Wheeler (1926–27).

respectively. It must be emphasized that the linear relationship is only valid in the above range. It is of incidental interest to note that the rates of increase of skull width on total length for female and male whales are not significantly different.

A measure of the high degree to which the association between skull width and total length approaches a linear relationship is given by the correlation coefficient which is as great as 0.87 for the females and 0.80 for the males. There is thus no justification for rejecting the hypothesis of an isometric relationship between the skull width and total length of the Mackintosh & Wheeler population. It is a justifiable inference to conclude that this isometric relationship holds for all populations of this species in which the total lengths lie in the range 14 metres to 24.3

metres. In particular it holds for populations in Areas I and II. It is therefore possible to deduce the lamination-number skull-width relationship from that holding between the lamination number and total length.

It is of some bearing on the above topic to compare the Mackintosh & Wheeler sample with the Area I sample for their common measurement of total length. The former population is truncated of several extreme small values so that the bottom limit for each sex in the two samples is the same. It has been necessary for ease of comparison to convert Mackintosh & Wheeler's small 1-metre length ranges to the mean value in feet. The figures are given below :

Male Fin Whale S. Georgia			Female Fin Whales S. Georgia	
Length	Number of measurements		Length	Number of measurements
55	6	.	—	—
58	7	.	58	6
61	13	.	61	11
64	45	.	64	9
67	78	.	67	30
70	45	.	70	36
73	3	.	73	38
77	1	.	77	8
80	—	.	80	1

The length frequency distribution of the specimens from Area I is given below :

Male Fin Whales Area I			Female Fin Whales Area I	
Length	Number of specimens		Length	Number of specimens
55	3	.	—	—
58	3	.	58	5
61	12	.	61	12
64	49	.	64	17
67	76	.	67	30
70	26	.	70	60
73	2	.	73	30
77	0	.	77	7
80	—	.	80	1

Inspection of the above lists of measurements shows that the length frequencies of both samples are arranged more or less symmetrically about the mean lengths. The mean lengths and standard deviation for the two samples were found to be :

					Mean length		Standard deviation
S. Georgia	.	.	Males	.	66·0	.	3·6
Area I .	.	.	,,	.	66·0	.	3·1
S. Georgia	.	.	Females	.	68·7	.	4·6
Area I .	.	.	,,	.	68·6	.	3·3

It is obvious that the two samples are remarkably alike in their distribution of the total lengths. On the other hand the 38 female and 23 male specimens caught in Area II give the following value :

			Mean length		Standard deviation
Area II .	.	Females	.	70·1	.	4·5
Area II .	.	Males	.	67·0	.	3·7

Although as shown by a " *t* test " the differences in mean total length between the Area II and the Area I whales are not significant at the 95% level there is some slight evidence for suspecting that the mean total lengths of both sexes in Area II are approximately 1 ft. greater than those in the Area I sample. The values of mean total length given above are only valid over the length range 55 ft. to 80 ft. and would be rather lower over the whole length range of the population.

The Lamination Number–Body-length Relationship

In Text-figs. 3 and 4 the lengths of males and females from Areas I and II respectively have been plotted against the lamination number. Certain facts which will be examined in detail are given below :

(*a*) There is considerable variation in length at every lamination number.

(*b*) At every lamination number the average length of the females is greater than that of the males.

(*c*) The average length per lamination number of the specimens from Area II is greater than that of the specimens from Area I.

(*d*) After the formation of the eighth lamination the number of individuals in each laminar group is inversely related to the number of laminations.

The mean body length for each lamination group is given in the following tables :

Sample Area I

	Female Fin Whales			Male Fin Whales	
Lamination number	Number of specimens	Mean length in ft.		Number of specimens	Mean length in ft.
3½	.	—	—	.	1	55
4	.	—	—	.	2	69
5	.	1	58	.	—	—
6	.	4	65·75	.	1	64
7	.	8	64	.	2	58
8	.	6	61	.	2	64
9	.	11	64	.	8	63·4
10	.	9	65	.	5	63·4
11	.	6	65	.	3	63
12	.	8	67·7	.	5	64
13	.	3	67	.	8	66
14	.	7	69	.	9	65·3
15	.	3	70	.	5	66
16	.	8	72	.	9	66
17	.	3	71	.	7	67
18	.	4	71	.	1	69

Sample Area I—cont.

Lamination number	Female Fin Whales		Male Fin Whales	
	Number of specimens	Mean length in ft.	Number of specimens	Mean length in ft.
19	1	74	2	66
20	5	71	5	66
21	1	74	2	70
22	4	71	5	68
23	1	73	7	67
24	8	72	5	67
25	2	71	3	66·6
26	6	72	3	67
27	3	72	2	65
28	2	71	3	66·3
29	2	68·5	2	69
30	1	73	4	66·5
31	1	70	2	66·5
32	5	74	1	65
33	1	75	1	70
34	2	—	1	71
35	1	75	4	66
36	6	72	1	68·5
37	1	76	1	65
38	—	—	1	67
39	1	73	1	69
40	5	71	2	68·5
41	—	—	—	—
42	2	73	1	66
43	1	69	3	66·5
44	—	—	2	66
45	1	72	1	68
46	1	75	2	67
49	—	—	1	67
50	2	75	3	67
52	—	—	2	66
53	—	—	1	65
54	2	76	3	66
55	1	69	1	66
56	3	71	2	64
58	—	—	2	66·5
59	—	—	1	67
60	—	—	2	69
61	—	—	1	68
62	—	—	1	73
63	—	—	1	70
66	—	—	1	65
67	—	—	1	70
70	1	75	1	71
71	—	—	1	65
75	—	—	1	68
76	—	—	2	66·5
80	1	73	—	—
83	—	—	1	64
85	—	—	1	64

Sample Area II

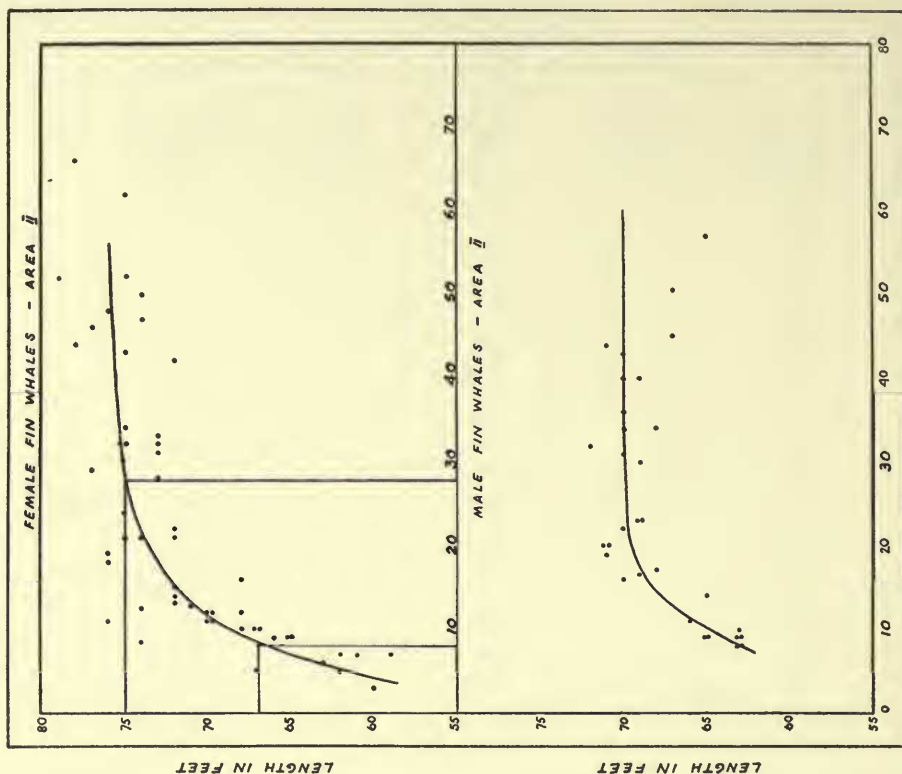| Lamination number	Female Fin Whales		Male Fin Whales	
	Number of specimens	Mean length in ft.	Number of specimens	Mean length in ft.
3	1	60	—	—
4	—	—	—	—
5	2	64·5	1	55
6	1	63	—	—
7	3	61	—	—
8	1	74	2	63
9	3	65·5	4	64
10	3	67	1	63
11	3	72	1	66
12	5	70·6	—	—
13	1	72·0	—	—
14	1	72	1	65
15	1	72	—	—
16	1	68	2	69·5
17	—	—	1	68
18	1	76	—	—
19	1	76	1	71
20	1	72	2	71
21	3	73·6	—	—
22	2	72·5	1	70
23	—	—	2	69
24	1	75	—	—
28	1	73	—	—
29	1	77	—	—
30	1	75	1	69
31	1	73	1	70
32	3	75	—	72
33	1	75	—	—
34	1	75	2	68
26	—	—	1	70
38	1	68	—	—
40	—	—	2	69
42	1	72	—	—
43	1	75	1	70
44	1	78	1	71
45	—	—	1	67
46	1	77	—	—
47	1	74	—	—
48	1	76	—	—
50	1	74	1	67
52	1	75	—	—
53	1	79	—	—
59	—	—	1	65
62	1	75	—	—
63	—	—	1	76
66	1	78	—	—
76	—	—	—	63

FIG. 4. The ear-plug lamination number—body length relationship of a population of Antarctic Fin Whales *Balaenoptera physalus* captured during 1955–56.
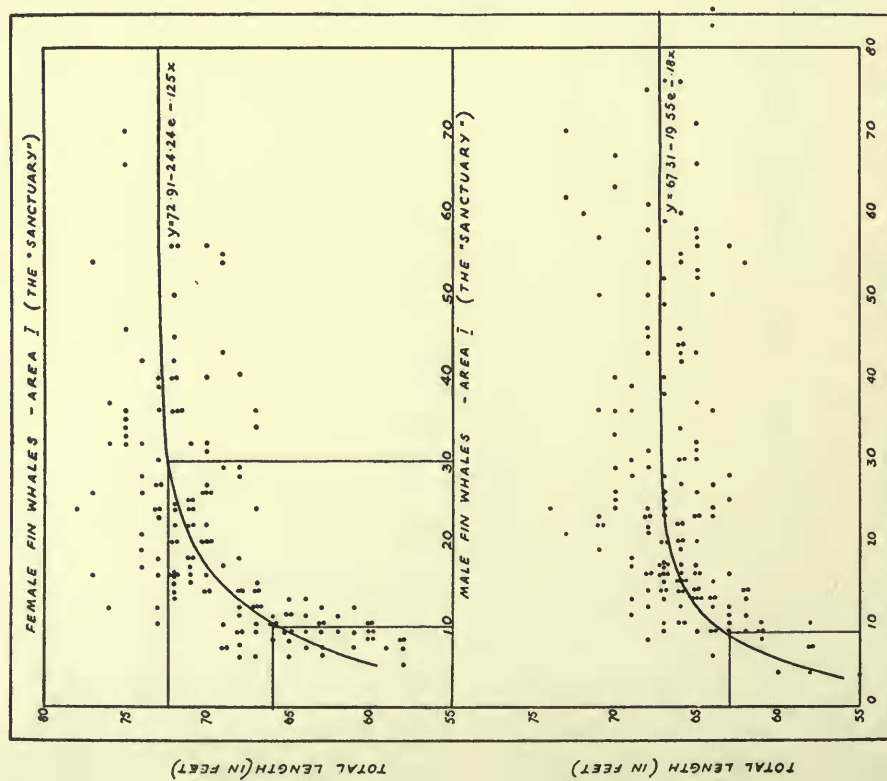
FIG. 3. The ear-plug lamination number—body length relationship of a population of Antarctic Fin Whales *Balaenoptera physalus* captured during 1955–56.

Text-figs. 3 and 4 suggest that for each sex, whales with more than 13 laminations are such that their total lengths are almost independent of their lamination numbers, i.e. the correlation coefficient between lamination number and length is not greatly different from zero for whales with more than 13 laminations in the ear plug. This correlation coefficient was evaluated as 0·169 for females and 0·27 for males in Area I. Using $t = r \sqrt{\dfrac{(n-2)}{(1-r^2)}}$ as a t-variate where " r " and " n " are the correlation coefficient and the number of individuals in the sample respectively, both of the above coefficients were found to be not significantly different from zero. This same analysis applied to the Area II whales revealed that as in Area I the lamination number was nearly independent of total length for whales with more than 13 laminations, i.e. for any Fin Whale with a lamination number greater than 13 the specific value of its number can be considered to have little bearing on its total length and skull width.

If any one plug is measured from its base to each successive lamination the increase in core length is found to take the form of an exponential curve like that which was described by Purves (1955), but the total length of the core for any one lamination number varies very greatly from one specimen to another, and cannot be used even as a rough guide to the lamination number. An average growth curve has been obtained (Text-fig. 5) by plotting the mean length of the core per lamination number at every fourth lamination against the lamination number. These mean core lengths are remarkably similar in the two sexes notwithstanding the difference of over 4 ft. in the adult body lengths between males and females. The curve appears to show that plugs of high lamination number are disproportionately long, but this effect may be due to the small number of plugs of high lamination number in the sample. If high lamination number is an indication of old age the presence of these disproportionately long plugs may be due to the mixing of populations owing to lateral migration Brown (1954). It will be seen at once that this growth curve is in no way comparable with that of skull width against body length so that neither the lamination number nor the plug length have any close relationship to the body length and skull width. It must, therefore, be concluded that the growth of the plug is independent of that of the body as a whole, and that its laminated core forms part of a rhythmic growth system which was initially established in response to one or more of a number of factors involving the passage of time, such as the breeding cycle, migratory movements, nutritional changes, temperature variation or inherent mammalian moulting cycles. The periodicity of the rhythm may vary from one individual to another but in a population with a very regular cycle of behaviour the variation is likely to be very small. Since the growth of the plug is not conditioned by the skull dimensions, it is possible that the shape of the bony meatus is continually adjusted to the growth increments, that there is no resorption of any part of the plug, and that the laminations constitute a complete record of the periodic desquamations from birth to death. In this connection it is of interest to draw attention to the difference between the growth of the ear plug in whales and that of the cycloid and ctenoid scales of fishes. Van Oosten (1955) states that in the fishes cessation of body growth ultimately ends in suspensions of scale formation. He continues

" In maintaining coverage of the body the scales have been found to grow at an approximately fixed ratio with the fish. The growth of the scale, is therefore, more or less a replica of that of the body. This fact has made possible the employment of scales in estimating the past growth of an individual. Multiplying the ratio of the length of that part of the scale that was completed at the end of a certain year of life to the final length of the scale by the length of the fish gives the estimated length
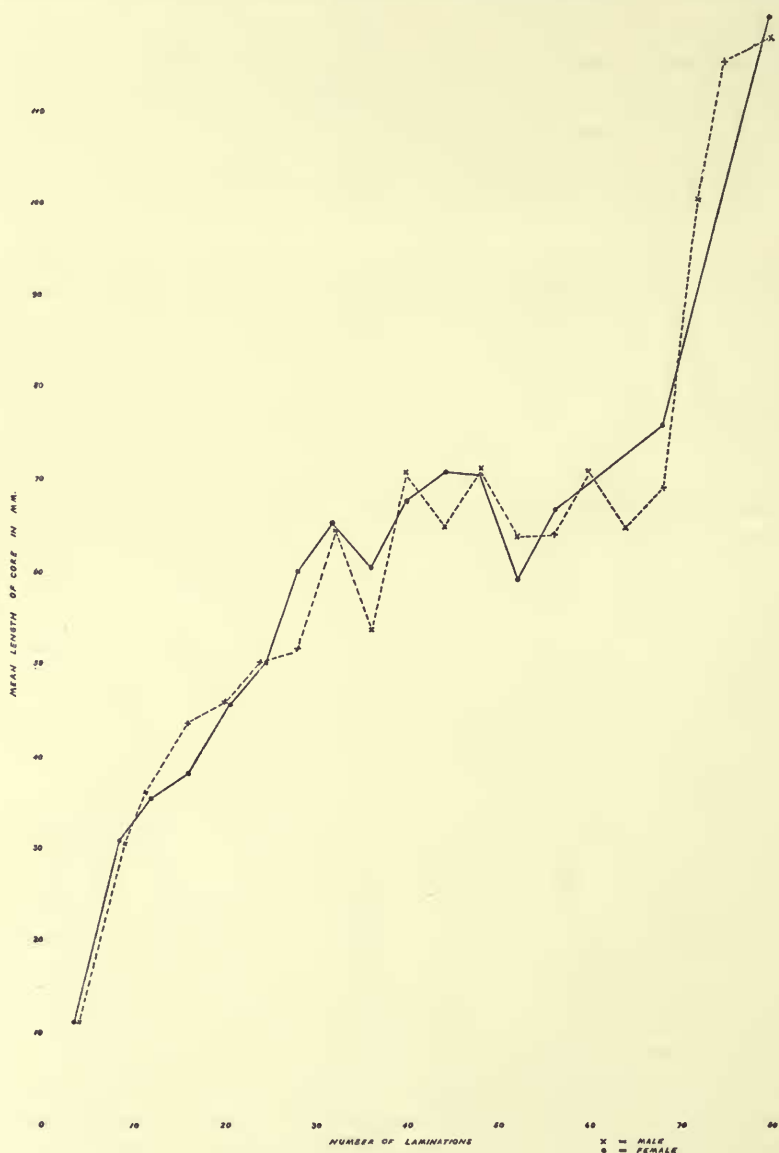

FIG. 5. Lamination number-core length relationship of the ear-plugs of a sample of Fin whales *Balaenoptera physalus*.

that the individual attained at that particular age.   Yearly increments of growth can be obtained by subtracting the different computed lengths ".   A similar system of length estimation based on the thickness of ear plug laminae could be arrived at with some difficulty in respect of whales under 6 years of age, but for animals above this age no correlation is possible.   Van Oosten also states that age determination in fishes permits studies on variation in growth rate with species, latitudes and different bodies of water.   " By observing the time of formation of laminae the length of growing seasons may be determined."   It is very doubtful whether environmental conditions have any direct influence on the time of formation of the laminae of the ear plug in whales, although nutritional conditions may to some extent determine their thickness.   Since there is strong evidence that lamina formation is an inherent moulting cycle it is very probable that it takes place whether the whale migrates or not.   If the rate of moulting can be established the ear plug would probably be a more accurate age indicator than the fish scale.

Since it was shown by Laws & Purves (1956) that up to the formation of the 12th lamination a fairly close correlation exists between body length and lamination number and in the present paper that after the 13th lamination the correlation coefficient approaches, but is not precisely, zero, it might be expected that an exponential growth function could be demonstrated over the whole range of laminations.

In Text-fig. 3 curves of mean total length against lamination number have been fitted by the method of least squares to the samples of males and females from Area I.   Dealing first with Area I females it was found that if " y " (in feet) is the length and " x " is the lamination number then a good fit to the data is given by

$$y = 72 \cdot 91 - 24 \cdot 24 \ \exp \ (-0 \cdot 125x)$$

where " exp " is the exponential function.   This expression is a description of the data only over the lamination range 6–80 and gives a growth curve from 61·5 ft. at 6 laminations to a maximum length of 72·91 ft.; extrapolation beyond these limits is not justified but Mackintosh & Wheelers' (1929) curve of immature body lengths can be used to complete the curve.[1]   It may be noted that a length of 71·9 ft. is attained at the formation of the 26th lamination.   The line in the graph (Text-fig. 3) represents the growth function, which is such that at any given lamination number the growth rate is proportional to the " remaining size " i.e., the maximum size minus the size reached.   A similar growth curve was fitted to the males Area I (Text-fig. 3) and a good fit was obtained by the curve

$$y = 67 \cdot 31 - 19 \cdot 55 \ \exp \ (-0 \cdot 18x).$$

Here again the curve only describes the growth in the range 6–80 laminations. The estimated length of 60·7 ft. at 6 laminations increases to an average maximum of 67·31 ft.   The length of 66·3 ft., one foot less than the maximum is achieved at about the 16th lamination.   The points marked on the 2 diagrams are the mean values of the lengths for each lamination number.   This result is in accordance with previously established information regarding the difference in the growth rates

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[1] Because of the under-representation in the sample of the 6th lamination group the first part of the growth curve may give an over-estimation of the average body length in this group, see page 149.

between male and female Fin Whales and both curves approximate to the average mammalian growth curve. It will, therefore, be assumed that the laminations are laid down at fairly regular intervals throughout the life of the animal.

The Rate of Formation of Laminae

In order to establish the rate of formation of the laminae, use can be made of the following information :

(a) The lowest number of laminae formed when the majority of the females are either lactating or pregnant.
(b) The lowest number of laminae formed when the vertebral epiphyses are ankylosed to the centra in the majority of adults.

The difference between these two figures will represent the approximate number of laminae formed between sexual and physical maturity which by deduction from Wheeler's (1929) figure of 15 corpora lutea accumulated in the ovary and Laws' (1955) rate of 1·4 per annum for their accumulation should be approximately 10 years.

In Text-figs. 6 and 7 each horizontal line represents the vertebral column and can be considered to be divided into four sections containing the anterior thoracic, posterior thoracic, lumbar and caudal vertebrae respectively. Each vertebral column or portion of a vertebral column has been placed in one or more of the vertical divisions according to the state of fusion of the vertebrae. A category described as " Fused Joint Visible " was given in the original data but for the purpose of the charts it was assumed that if the joint was visible it must also contain a thin layer of cartilage, so vertebrae in this category were placed in the division labelled " Unfused Fine Cartilage ". The horizontal lines in Text-fig. 6 have been thickened to denote whales which were known from the data to be pregnant.

The horizontal lines which completely traverse the charts are drawn through the lamination numbers above which the vertebral epiphyses are fused and invisible in the majority of individuals, and through the number in the chart of the female whales above which the majority are pregnant. It will be seen from Text-fig. 6 that the number of laminations shown between these two lines is 20 so that if the estimated period between sexual and physical maturity is 10 years the rate of lamination formation is approximately 2 per year.

As a check on the above result it may be noted that Mackintosh & Wheeler's figure for the length of female Fin Whales at sexual maturity is 66 ft. This figure has been confirmed by Peters (1939), Mackintosh (1942), Brinkmann (1948), Nishiwaki & Hayashy (1950), the length at physical maturity being in the region of 72·4 ft. The regression line of growth (Text-fig. 3) passes through these two lengths at the 10th and 30th lamination respectively. If the period between sexual and physical maturity is 10 years the rate of accumulation of laminae is 2 per year. When the figures of Nishiwaki & Oye (1951) and Jonsgård (1952) of 67 ft. at sexual maturity and 75 ft. at physical maturity are applied to the growth curve of the Area II females (Text-fig. 4) they are seen to cut the curve at the 8th and 28th lamination respectively.

Here again if the period between sexual maturity and physical maturity is 10 years then the rate of accumulation of laminae is 2 per year.

Up to date no collection of Blue Whale ear plugs large enough for statistical analysis has been received but from inspection of the few specimens which were collected by Simons (1956) there is no reason to conclude that the rate of accumulation of laminae differs greatly from that estimated in the Fin Whale ear plugs. In this connection a letter received from A. H. Laurie is quoted below :

" Your query as to the interpretation of the figures given in my paper (Laurie, 1937) has resulted in the unearthing of an error which appears to have lain unnoticed for twenty years. On page 250 I have shown that the annual increment of corpora lutea, now called corpora albicantia, appears to be slightly in excess of one per annum. The average figure given was 1·13.

" As is seen in the tables, the above conclusion is based on samples containing three categories of whale, namely pregnant, resting (i.e. neither pregnant nor having recently ovulated), and non-pregnant but having recently ovulated.

For convenience I reproduce here the totals in this argument :

Percentage pregnant		Percentage resting		Percentage recently ovulated
64	.	24	.	12

" Where the mistake arises, and I have repeated it categorically in section 6 of the Summary (p. 268) is that I have taken the annual increment to apply to the whole adult stock of female Blue Whales. At the same time no account has been taken of that fraction of the stock which was lactating, and thereby absent from the sample. To clarify this statement let us add a hypothetical but plausible number to the above percentages, to include the absent lactating whales and let us assume that the number of lactating whales corresponds to a similar percentage of pregnant whales in the previous year. The total stock is then represented by 100 (as above) plus an additional 64.

" The total is thus 164, of which the additional 64 just added, being in lactation can be presumed not to have ovulated during the year under review. It follows therefore that the figure given for annual increment of corpora albicantia must be corrected thus :

$$1\cdot13 \times \frac{100}{164} = 0\cdot69.$$

" Another way of stating the amendment is to say what I should have said in the first place, namely that the average increment in corpora lutea per *breeding cycle* is 1·13.

" If we now employ the revised figure of 0·69 c.l. per annum for Blue females as a whole, the putative time scale can be revised as follows.

" Physical maturity was shown to coincide with the accumulation of 11 corpora. After allowing 1·91 corpora for the first breeding season, i.e. to include

WHALE NO.	LAM. NO.	UNFUSED THICK CARTILAGE	UNFUSED FINE CARTILAGE	FUSED JOINTS INVISIBLE
358	80			
700	70			
2009	66			
1352	56			
1703	55			
1250	54			
1435	50			
706	46			
438	45			
2130	43			
1042	42			
2085	42			
488	40			
1704	40			
937	40			
2015	40			
1044	40			
6670	38			
1931	37			
1669	36			
593	36			
2007	36			
1933	36			
741	36			
780	35			
482	34			
1633	36			
1234	32			
486	32			
1710	32			
672	32			
1280	30			
1968	30			
747	29			
1169	29			
743	28			
1704	27			
1625	27			
478	26			
1358	26			
867	26			
2099	26			
745	26			
749	25			
398	24			
434	24			
1366	24			
603	24			
700	24			
1892	24			
1788	24			
894	24			
1793	23			
714	22			
2122	22			
1779	22			
1083	22			
646	21			
597	20			
898	20			
1964	19			
1085	18			
2136	18			
869	18			
784	18			
1854	17			
737	17			
513	17			
1823	16			
703	16			
855	15			
1811	15			
1079	14			
906	14			
1784	14			
1968	14			
2128	14			
656	14			
670	13			
2094	12			
786	12			
1034	12			
1320	12			
448	12			
1208	12			
1167	12			

1165	11
935	11
1817	10
1821	11
1890	11
1937	11
1196	10
1279	10
859	10
1247	10
1898	10
1749	10
519	10
1813	9
1036	9
1248	9
118	9
933	9
1108	9
1748	9
2126	9
1930	9
1864	9
2059	9
1454	8
871	8
1856	8
776	8
652	8
707	8
601	7
648	7
1819	7
1785	7
739	7
1200	7
2013	7
1820	6
352	6
1714	6
863	6
1284	5

FIG. 6. State of fusion of the vertebral epiphyses of a sample of female antarctic Fin whales *Balaenoptera physalus*. Each horizontal line represents a vertebral column which can be considered to be divided thns $\underline{\quad AT \quad PT \quad L \quad C \quad}$ where AT = anterior thoracic PT = posterior thoracic, L = lumbar, C = caudal. The thick lines represent individuals which were known to be pregnant.

a period of $2\frac{1}{2}$ years from birth, the remaining 9·1 corpora could represent 13·2 years so that the age at physical maturity now becomes 2·5 + 13·2 = 15·7 years, instead of 10 to 11 years. The oldest whale in my collection was approximately 45 instead of 30.

" I must emphasise that the above figures relate to the ' ovary clock ' of more than twenty years ago. In view of the much higher percentage of pregnancy now observed in whale samples, the regulator of the clock has apparently been altered, presumably by external influences."

It will be noted that the age at physical maturity for Fin Whales was assessed at 15 years and that the oldest specimen recorded in the present sample was $42\frac{1}{2}$ years old. From the ear plug and ovary data therefore, both Fin and Blue Whales appear to become physically mature at the same age and it may be presumed that they have much the same maximum life span.

Regarding the male Fin Whales the evidence is rather less conclusive. According to Jonsgård (1952) " the various investigations show that these attain sexual maturity

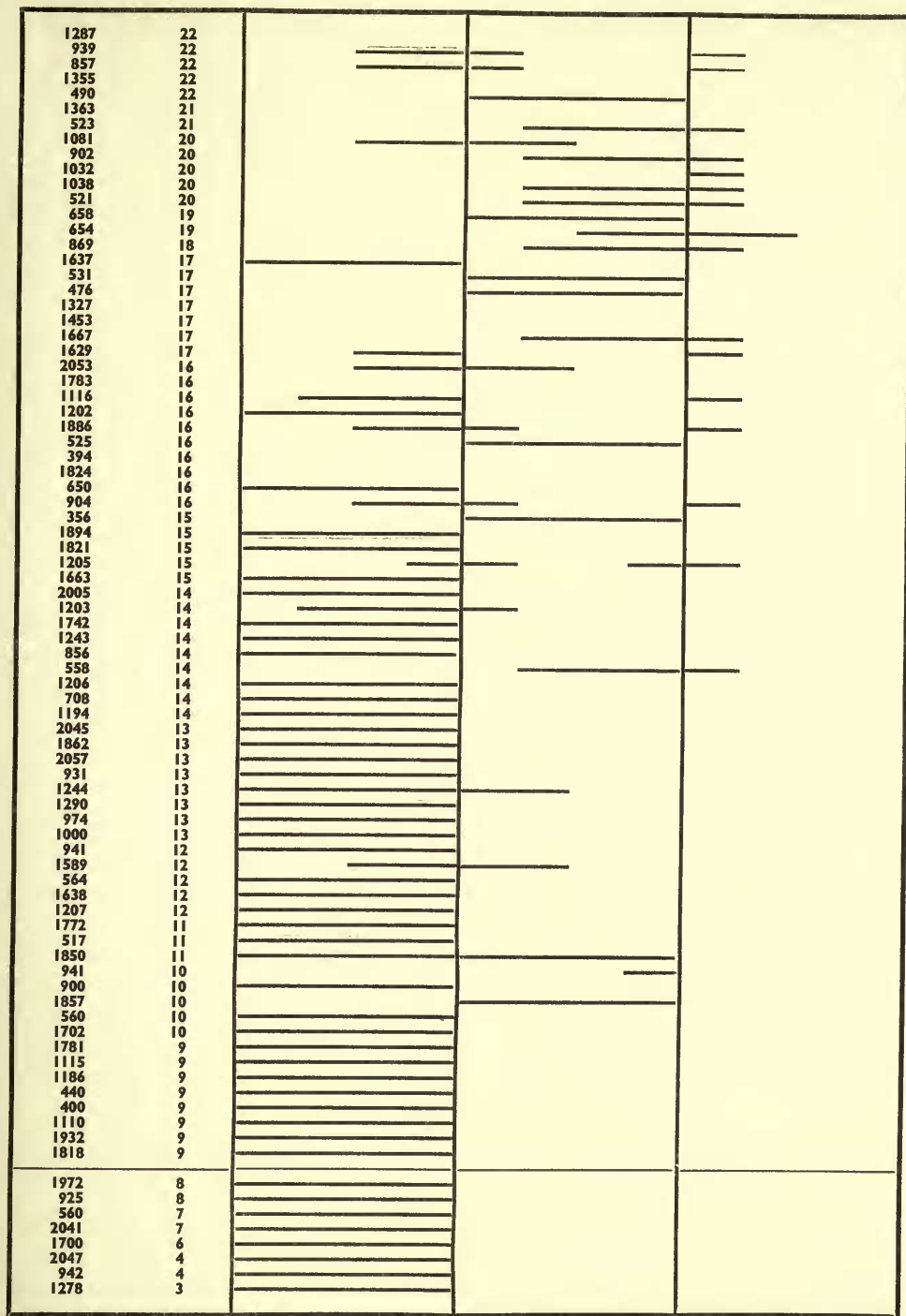| WHALE NO.	LAM. NO.	UNFUSED THICK CARTILAGE	UNFUSED FINE CARTILAGE	FUSED JOINTS INVISIBLE
675	83			—
1075	85			—
788	76			—
570	76			—
446	75			—
1120	71			—
1252	70			—
702	67			—
527	66			—
1356	63			—
1705	62			—
1855	61			—
1673	60			—
462	60			—
396	59			—
1744	58			—
1741	58			—
406	56			—
1627	59			—
1636	56			—
442	59			—
605	55			—
1113	54			—
1077	54			—
568	54			—
710	53			—
1978	52			—
1776	52			—
1745	50			—
1452	50			—
1112	50			—
1825	49			—
1860	46			—
1258	46			—
716	45			—
1121	44			—
1198	44			—
1326	43			—
976	43			—
927	43			—
1365	42			—
7861	40			—
1671	40			—
	40			—
1626	39			—
361	38			—
1597	37			—
1240	36			—
1450	36			—
1893	36			
1666	35			
1423	35	—	—	—
2120	32		—	
1207	31			
2083	31		—	—
1815	31	—		—
1888	30		—	
1740	30			
772	30		—	—
704	30		—	
1239	29			
1965	29			
1111	28			
1599	28		—	—
2051	28		—	—
945	27		—	
1822	26			
1743	26			—
1674	26			
1251	25			
1296	25		—	
363	25			
1274	24	—		—
1451	24			
1071	24			
480	24		—	—
1635	24		—	
2049	23	—		—
1902	23	—		
2087	23		—	—
1774	23		—	
2132	23		—	—
1777	23			
1325	23			

FIG. 7. State of fusion of the vertebral epiphyes of a sample of male antarctic Fin whales *Balaenoptera physalus*. Each horizontal line represents a vertebral column which can be considered to be divided thus | AT , PT , L , C | where AT = anterior thoracic, PT = posterior thoracic, L = lumbar, C = caudal.

at about 63 ft." The length at physical maturity has been ascertained at approximately 68 ft. by Mackintosh & Wheeler, Peters, Brinkmann, Nishiwaki & Hayashi. In Text-fig. 3 the growth curve of the male whales cuts the 63 ft. ordinate at the 9th lamination, but the upper part of the curve is almost horizontal and covers a wide range of lamination numbers at the average maximum length of 67·31 ft. Referring to the chart (Text-fig. 7) it will be seen that all the vertebral epiphyses are fused after the 36th lamination but as only two individuals are represented in the sample corresponding to the four numbers preceding 36, the actual number formed at physical maturity may be as low as 31. If the rate of laminae formation is approximately 2 per year the male whales would appear to become sexually mature earlier than the females but take longer to become physically mature.

The most recently established data about the ages of sexual maturity are those of Nishiwaki (1952) who quotes $3\frac{1}{2}$ years for males and 4 years for females. The present investigation gives a figure of $4\frac{1}{2}$ years for males and 5–6 years for females. The discrepancy in these two results could be accounted for if the two most distal ear plug laminae could be regarded as being present in the foetus, i.e., the remnant of the epitrichium and the vernix caseosa. Against this hypothesis is the evidence of the ear plug of a 50 ft. long male, collected at Steinsham in 1955. This ear plug had only two laminae, one of which was the "foetal cone" Purves (loc. cit.) and was estimated by Laws & Purves (loc. cit.) to be one year old, and by Ruud, from inspection of the baleen plates to be $1\frac{1}{2}$ years old. The animal was of course much too long to be newly born. According to Sharpey-Schafer (1929) the vesicular cells of the epitrichium are shed late in the intra-uterine life and mingle with the secretion of the sebaceous glands to form a waxy covering, the vernix caseosa. The foetal cone of the ear plug is always very small, undifferentiated, mis-shapen, waxy and in the general appearance could represent the vernix caseosa. The penultimate lamination on the other hand, is always the deepest in the whole series and much too coarse to be present in the foetus. On the basis of the above estimation it represents from 1–$1\frac{1}{2}$ years' desquamation during the suckling and first free feeding life of the calf. The discrepancy could also be accounted for if the whales outside the "Sanctuary" become sexually mature earlier than those in Area I.

It may be argued that the ovaries and baleen plates constitute an uncertain guide to the rate of formation of the laminae of the ear plug, so some alternative rates of formation must now be considered. In the first instance it must be stated that the extremely regular appearance of the laminae and the smooth, typically mammalian exponential growth curve afforded by plotting length against lamination number in both sexes of both samples preclude any possibility of a grossly irregular rate of desquamation. It is difficult to conceive of any cyclic phenomenon in the biology of whales or any other mammal for that matter which could account for three moults or desquamations per year. Whales like most other mammals are subject to a bi-annual rhythm of seasonal change and all the accumulated observations on their natural history suggest that their biology and physiology are adjusted accordingly. Any idea of an *average* rate of three desquamations per year derived from an irregular desquamation rate is precluded by the extremely regular appearance of the laminae. If four or more laminations per year are considered than the evidence of the ear

plugs collected at Steinsham have some bearing on the problem. In that collection there was one plug (above cited) with only two laminations, one of which was the foetal cone. If the rate of formation of laminae had been four per year then that animal had grown from 21 ft. to 50 ft. in six months, and yet should theoretically have just been weaned at the time of capture. Now the length at weaning, of the Antarctic Fin Whale has been established by Mackintosh & Wheeler (1929) at 39 ft. and since the North Atlantic Fin Whale is known to be smaller than the Antarctic form the average length at weaning of the former is likely to be less than 39 ft. A similar argument could be used for four of the Blue Whales represented in the present collection of ear plugs, since they possessed only two laminations and yet all the animals were over 70 ft. in length, i.e. some 20 ft. above the established length at weaning of the Blue Whale.

Any rate of formation of laminae greater than four per year can be discounted on the basis of the above argument and there is left for consideration the idea of the formation of a single lamination per year.

Assuming the formation of one ear plug lamination per year in the present sample, the ages at sexual and physical maturity of the female Fin Whales would be 10–12 years and 30 years respectively and the oldest specimen some 85 years old. These figures are quite inconsistent with any of the previously assessed ages and growth rates of Fin Whales but are comparable with those in Man and require some critical examination. In the first instance it may be stated that the broad distal lamination was estimated to represent the combined weaning and first free feeding period of the animal's life, i.e. a period of approximately one year. The end of this period would correspond with the time of maximum blubber thickness for that year and would be followed by the northerly migration. If the subsequent desquamation of the whole body followed fluctuations in blubber thickness from year to year, the laminations of the ear plug would be formed annually. If, as seems likely, the ear plug is concerned in the conduction of sound from the blind end of the external auditory meatus to the middle ear, a desquamation rate correlated with blubber thickness would seem to be a necessity

Reverting once more to the subject of ovaries—all authors are agreed that the onset of physical maturity corresponds with accumulation of 15–16 corpora lutea albicatia. If Rund's figure of 1·6 corpora lutea per two years be used as the accumulation rate instead of that of Laws then the period between sexual and physical maturity would be 20 years and not 10 as previously estimated. In the absence of any definite proof of the rate of formation of the ear plug laminae, it can only be stated that the evidence shows conclusively that the rate is either one or two per year and that the latter is more consistent with all the previously accumulated knowledge of the natural history of Fin whales.

THE AGE DISTRIBUTION

Having accepted provisionally the validity of the hypothesis that the rate of increase in lamination-number is two per year, it is possible to form an age-frequency sample distribution from the sample frequencies of the lmination numbers. If " c " represents lamination number and, if it is assumed that the $2i^{\text{th}}$ lamination is

first recognizable approximately on the ith birthday, e.g. the 14th lamination on the 7th birthday, and the $(2i-1)^{th}$ lamination approximately at age $(i-\frac{1}{2})$, then it is seen that whales with $2i$ laminations are between the ages of i and $i+\frac{1}{2}$ years and whales with $(2i-1)$ laminations between the ages of $(i-\frac{1}{2})$ and i years. The sum of the two frequencies of lamination- numbers $(2i-1)$ and $2i$ is thus the sample
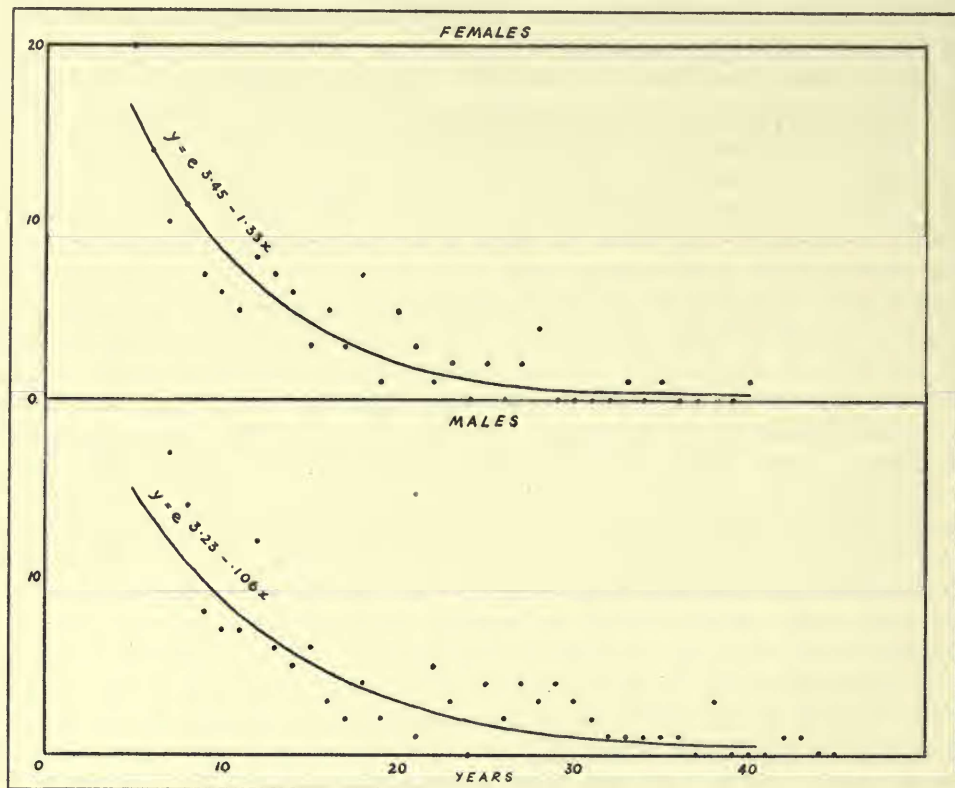
FIG. 8. Smoothed age frequency distribution of a sample of fin whales *Balaenoptera physalus*

frequency of the one year group of individuals whose nearest birthday is i years. In the case of the females sampled in Area I only the frequencies of lamination-numbers of 9 or more were used in the construction of the age-frequency distribution, it was considered, because of the corresponding smaller average total body lengths, that the smaller lamination numbers were not fully represented in the sample. The age-frequencies of the Area I females are shown in Text-fig. 8.

At the outset it must be emphasized that owing to the wide variability of the data, the small size of the sample and the possible lack of randomness of selection, due to differences in capture proneness, etc., no more is claimed for the ensuing analysis than that any conclusions based on it are but crude approximations of the true values of the population.

The simplest hypothesis to fit the data is that the mortality rate is constant, i.e. the probability that an individual will survive a further year is independent of its present age.   In this case the age frequencies follow a geometrical progression and the points on the graph of the frequency distribution lie on a curve of exponential form. Fitting by weighted least squares, the curve :

$$y = e^{3.45-0.133x}$$

was obtained, where x is the age in years and is seen in Text-fig. 8 to give a fairly good description of the sample frequencies.   This curve implies that over the given range of age 5 or more years a proportion $e^{-0.133}$ or approximately 88% of each year group survives to the following year.   The insensitive nature of this estimate of survival rate is demonstrated by its 95% confidence interval which ranges from 79% to 97%.

In order to discount the under-representation of the smaller whales the above survival curve was constructed using only the data for not less than 9 laminations at which according to the growth curve in Text-fig. 3 the mean length is 65 ft.   The same minimum average length is insured in the sample of males captured in Area I by using only the data of 13 or more laminations.   The age-frequencies for the Area I males are shown in Text-fig. 8.   As in the case of the females a weighted least squares exponential curve was fitted to the data and as is seen in Text-fig. 8 the curve :

$$y = e^{3.23-0.106x}$$

does reflect the characteristics of the sample frequencies.   This curve implies a survival rate of $e^{-0.106}$ or 90% for each year group.   There is apparently no evidence of a significant difference in survival rates between the two sexes.

Assuming the perhaps somewhat unreal hypothesis of a stable population, constant in size, it is possible to conjecture estimates of the immature females' mortality rate.   The estimation of this mortality rate will be made for each of the following four models of birth rate.

Model 1.   First offspring at approximately 5 years old with a succeeding birth rate of one offspring produced every 2 years.

Model 2.   First offspring at 6 years old with succeeding birth rate of one offspring every two years.

Model 3.   First offspring at 5 years old with succeeding birth rate of one offspring every three years.

Model 4.   First offspring at 6 years old with succeeding birth rate of one offspring every three years.

Under the conditions of Model I the expected number of female offspring, assuming that the birthrate is the same for the two sexes, is at the rate of one every 4 years. The total number of female offspring per year is then expected to be approximately :

$$\sum_{i=5} Bl(i) \times \tfrac{1}{4}$$

where $Bl(i)$ equals the number of females in the age group $(i - \tfrac{1}{2})$ to $(i + \tfrac{1}{2})$ years old.   If B is assumed to be the constant yearly number of female births, then $l(i)$

is seen to be the approximate probability that a female will survive to an age of i years. Equating the two expressions of total yearly female births

$$\sum_{i=5} Bl(i) \times \tfrac{1}{4} = B$$

it follows that

$$\sum_{i=5} l(i) = 4.$$

Now the survival probabilities $l(i)$ are estimated as being proportional to the yearly ordinates of the fitted age distribution curve $y = e^{3.45-0.133x}$
i.e.

$$l(i) = \frac{4\,yi}{\sum\limits_{i=5} yi} \qquad\qquad (i > 5)$$

where

$$yi = e^{3.45-0.133i}.$$

The survival probabilities for the other 3 models may similarly be obtained and the numerical values of the $l(i)$ for all 4 models are tabulated in Table I. Thus, for example, it is seen from this table that under the conditions of Model I there is

TABLE I.—*Provisional Mortality Rates of Antarctic Fin Whales*

Age i	Observed frequencies	Fitted frequencies	Model 1 100 $l(i)$	100 $d(i)$	Model 2 100 $l(i)$	100 $d(i)$	Model 3 100 $l(i)$	100 $d(i)$	Model 4 100 $l(i)$	100 $d(i)$
Under 5	—	—	—	50·0	—	—	—	25·0	—	—
Under 6	—	—	—	—	—	50·0	—	—	—	25·0
5	20	16·130	50·0	6·2	—	—	75·0	9·4	—	—
6	14	14·116	43·8	5·5	50·0	6·2	65·6	8·2	75·0	9·4
7	10	12·353	38·3	4·8	43·8	5·5	57·4	7·1	65·6	8·2
8	11	16·810	33·5	4·2	38·3	4·8	50·3	6·3	57·4	7·1
9	7	9·460	29·3	3·6	33·5	4·2	44·0	5·5	50·3	6·3
10	6	8·279	25·7	3·2	29·3	3·6	38·5	4·8	44·0	5·5
11	5	7·245	22·5	2·8	25·7	3·2	33·7	4·2	38·5	4·8
12	8	6·340	19·7	2·5	22·5	2·8	29·5	3·7	33·7	4·2
13	7	5·548	17·2	2·1	19·7	2·5	25·8	3·2	29·5	3·7
14	6	4·855	15·1	1·9	17·2	2·1	22·6	2·8	25·8	3·2
15	3	4·249	13·2	1·7	15·1	1·9	19·8	2·5	22·6	2·8
16	5	4·718	11·5	1·4	13·2	1·7	17·3	2·1	19·8	2·5
17	3	3·254	10·1	1·3	11·5	1·4	15·1	1·9	17·3	2·1
18	7	2·848	8·8	1·1	10·1	1·3	13·2	1·6	15·1	1·9
19	1	2·492	7·7	0·9	8·8	1·1	11·6	1·5	13·2	1·6
20	6	2·181	6·8	0·8	7·7	0·9	10·1	1·4	11·6	1·5
21–25	7	7·438	4·6	3·6	5·3	3·9	6·9	5·2	8·0	6·0
26–30	6	3·816	2·4	1·5	2·7	1·7	3·5	4·1	4·1	2·5
30–40	3	2·966	0·9	0·9	1·0	1·0	1·4	1·6	1·6	1·6

Note. The above mortality rates were calculated from the age frequency distribution of a single sample of the population using the ear plug lamination as guide to the age. The figures are based on an assumed rate of formation of 2 laminations per year. If the rate of formation is one lamination per year the age increments in column I would have to be doubled.

an estimated proportion of 50% surviving to an age of 5 years and a proportion of 25·7% surviving to an age of 10 years. The value $d(i)$ given in the same table are calculated from the relationship

$$d(i) = l(i) - l(i + 1)$$

and therefore 100 $d(i)$ is the estimated percentage of the population which dies between the ages of i and $(i + 1)$ years. Thus in Model 1 an estimated 5·5% die between the age of 6 and 7 years. From the columns of $d(i)$ it is seen that the immature mortality rates are such that 50% of the population dies under the age of 5 in Model 1, 50% die under the age of 6 in Model 2, 25% die under the age of 5 in Model 3, and in Model 4, 25% die under the age of 6. It is of some interest to note that if the fitted exponential curve is extrapolated backwards to age zero then the ensuing immature death rate is such that 48·7% of the population die under the age of 5 years, and 55% under the age of 6 years, values very close to that obtained under Models 1 and 2.

From the growth curve of Area I females (Text-fig. 3) it is seen that the fitted regression function estimates the mean total lengths at ages 3, 4 and 5 years as 61·5 ft., 64·0 ft. and 66·0 ft. respectively. As the whales prone to capture are restricted to a minimum length of 57 ft., there is a strong likelihood that the given mean values of total length of the 3- and 4-year-olds are over-estimates of the population values at these ages, but as the range of the sample of the 5-year-olds (9 and 10 laminations) is above 60·0 ft. there is no reason to believe that the estimation of this age group has been affected by the size restriction. If the population proportional frequencies of the 3 and 4 years old are assumed to be given by the extrapolated values of the exponential female age-distribution (Text-fig. 8) then as 5 3-year-olds and 14 4-years are present in the sample it may be inferred that approximately 23% of the 3-year-olds and 76% of the 4-year-olds are over 57 ft. in length, and thus prone to capture. As stated before, the sample evidence indicates almost conclusively that 100% of the 5-year-old age group are over 57 ft.

The figure for the percentage of immature whales in the total catch is, of course, dependent upon the age of attaining sexual maturity; this age is assumed to be 4 years in Models 1 and 3, and 5 years in Models 2 and 4. The numbers of females taken in Area I under the ages of 5 and 6 years are respectively 39 and 19 out of a total catch of 156 whales giving the percentage of immatures in the catch as 12·2 for Models 1 and 3 and 25·0 for Models 2 and 4.

CONCLUSIONS

The original hypothesis of a bi-annual rhythm for the formation of the laminae having been supported by correlation with observations on the growth of the baleen plates up to the sixth year of life it remained to establish whether this rhythm continued throughout the life of the animal.

It has been shown that the growth of the plug is not directly associated with the lateral growth of the skull, but that there is an exponential relationship between the total body length and the lamination number.

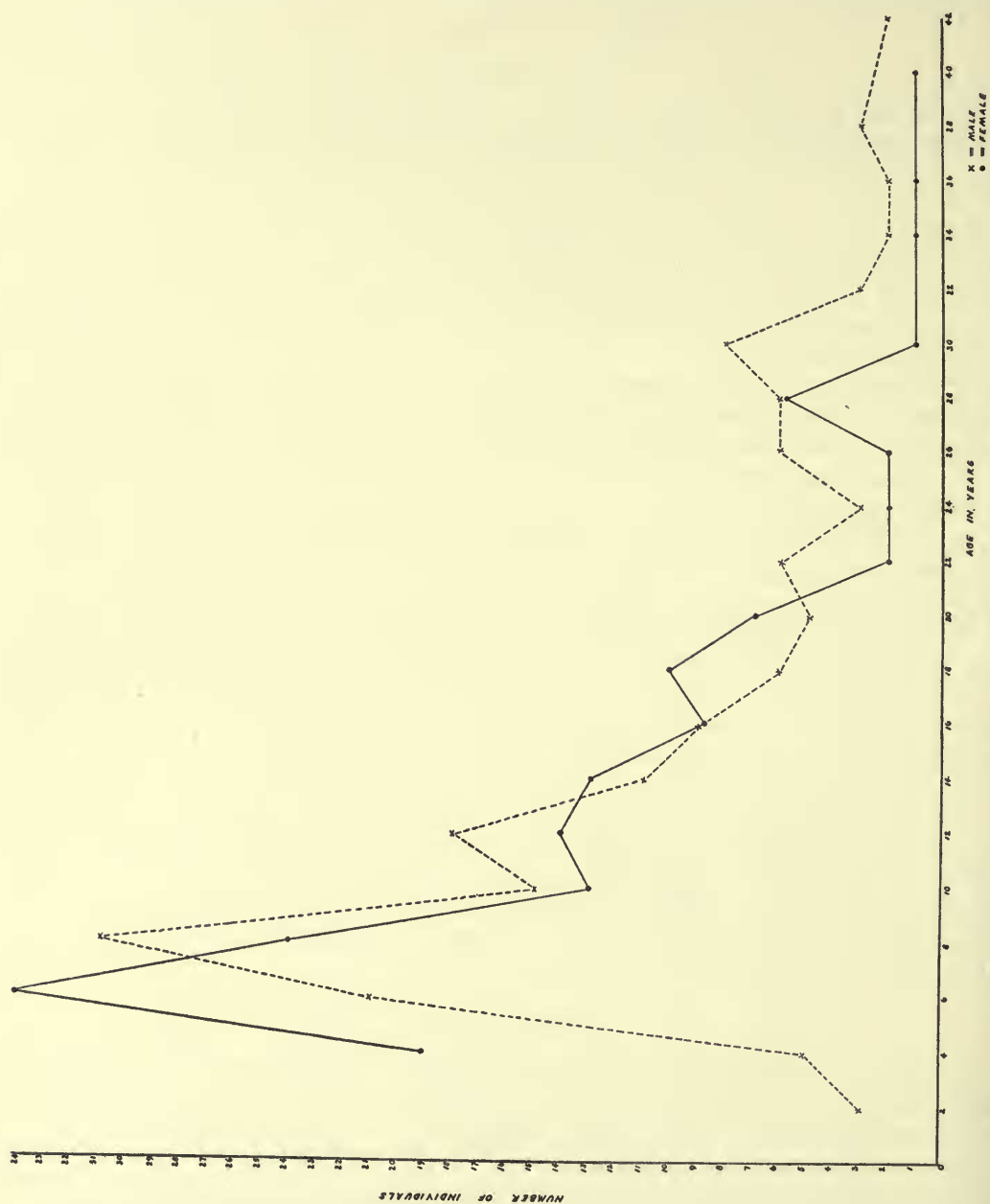The exponential growth curve of the body length approximates in form to the

FIG. 9. Age distribution of a sample of male and female antarctic fin whales *Balaenoptera physalus.*

normal mammalian growth curve and it was therefore assumed that the laminae of the ear plug were formed at regular intervals throughout life.

Assuming the interval between sexual and physical maturity to be 10 years as assessed from previously established information about the number and rate of formation of corpora lutea produced during this interval, it has been shown that the rate of formation of laminae is approximately 2 per year.

The previously established total body lengths of female Fin Whales at sexual and physical maturity, i.e., 66 ft. and 72·4 ft. respectively are identical with those deduced from the ear plug body length growth curve using the above rate of laminra formation.

The fact that the average core length per lamination number is almost identical in the two sexes, notwithstanding the difference in the skull proportions, indicates that the method of counting is fairly accurate.

Using the lamination number as a guide to age, the age frequency distribution of the sample takes the form of exponential curves in both sexes. From these exponential curves an age independent adult mortality rate of 12% per annum has been deduced for the female population, and 10% for the males.

The age dependent mortality rates for the female population have been tabulated using two different ages at sexual maturity and two durations of breeding cycle. Assuming the age at sexual maturity to be five years with the first offspring at six years the immature female mortality rate would be approximately 50%.

Assuming the above age at sexual maturity and that the Area I sample is representative of the catch then 25% of the catch is composed of immature specimens ; a figure which accords well with the average annual catch of immature animals and the expected proportion prone to capture under the existing regulations. It is interesting to note that the female adult mortality rate of S. Georgia population between the years 1925–31 was assessed by Wheeler (1934) at 13% per annum and the theoretical immature mortality rate at approximately 50% ; it will be seen that the adult female mortality rate for the present Area I sample was found to be in close agreement with these figures. With the age at sexual maturity at 5 years and the fertility rate 25% the above figures are exactly those required to keep the population stable in size. They also approximate to the figures for the apparent mortality rate which would be obtained by sampling an increasing population with a negligible mortality rate.

From the statistical analyses made by Hylen, Jonsgård, Pike & Ruud (1955) it may be noted that the peak catches are obtained according to the baleen plate data from age group 3 for females and age group 4 for males. According to the ear plug data from Area I the peak catches were obtained from the age groups 4–6 years in respect of females and 6–8 years in respect of males. This discrepancy may be partly explained by a difference between the mean total body lengths in the two populations, but is probably mainly due to the increased proportion of young animals in the population outside the " Sanctuary " the adult mortality rate of which was estimated to be 25%.

From the Hylen et al. analysis it appears that the population has become sexually mature at an earlier age in recent years. If Jonsgård's (1952) body length figure

of 67 ft. at sexual maturity is applied to the growth curve of the Area II sample it will be seen to cut the x ordinate at the 8th lamination giving an age at sexual maturity of 4 years.

The oldest specimen recorded in the present sample was 42 years old and in this respect it is necessary to draw attention to a paper by Simons (1957) in which he states that in an unmolested Humpback Whale population the life span was very low. He bases his comments on the fact that only a small proportion of his sample of 146 individuals had attained an age greater than 14 years and that only 1 had reached the age of 29. It will be noted that his sample size for both sexes is smaller than the Area I sample. Under the conditions of Model 1 only 13% of the Area I population is over 14 years old and only 2·4% over 25 years old; the latter figure embraces all ages between 26 and 30, so the figure for the 29-year-olds is more likely to be $\frac{1}{2}$%. These figures give no exact indication of the maximum life span of the animals. The question as to whether or not the material described in the present paper represents a random sample can be judged from Text-figs. 9 & 10. In Text-fig. 9 the age frequencies are plotted at intervals of two years, i.e. the approximate breeding cycle. It will be seen that males and females are present in each group in comparable numbers except that the peak value for males occurs two years later than that of the females. The left-hand side of the curve is much steeper than that of the right in both sexes notwithstanding that all the animals represented are above the permitted size limit. This effect is not due to any lack of randomness in the sample, nor to any length discrimination on the part of the gunners in the whaling fleet, both of which ideas have been suggested to explain the phenomenon in other samples. The steepness of the left-hand side of the curve is due to the fact that in the immature age groups the length variation is both relatively and absolutely greater than that of the adults, the standard deviation per age group in the sample being in the region of 5 ft.; thus a significant proportion of the immature animals is below the permitted size limit and therefore absent from the sample. As might be expected this effect is observable at a greater age in the males than in the females. In Text-fig. 10 the total frequencies of male and females have been plotted at two-yearly intervals. The dotted line represents the age frequency distribution of a hypothetical population of whales breeding every two years in which every individual becomes sexually mature at six years and in which the age frequency distribution remains stable with a constant mortality rate. Such a hypothetical population is perhaps unrealistic but the shape of the curve does indicate that the age frequency distribution of the sample approximates to that of a theoretically possible whale population. It is reasonable to assume that the sample is randomly drawn from a population with the above biological characteristics. If Simon's material is assumed to represent a truly random sample of the population then it would be statistically unlikely for more than one specimen in the sample of 146 females to be 29 years old, even if the maximum life span was 42 years or more.

Of the 12 Blue Whale ear plugs in the present collection only two were taken from animals more than 2 years old; 1 was from an animal 6 years old and the other 12 years old.

The above figures are based on the assumption that the ear plug laminae are

formed at the rate of 2 per year but with the possible formation of one lamination per year the values would have to be doubled. For the purpose of estimating changes in the population structure the actual rate of laminar formation would appear to be immaterial provided the error, if any, is constant from year to year and age group to age group. From this point of view the ear plug is probably a more reliable

FIG. 10. Age distribution of a sample of fin whales *Balaenoptera physalus*. Sample distribution = X. Theoretical population distribution = o.

guide to age than the ovary. The assumption on which the life tables were estimated i.e. that the size of the population is a constant number from year to year, is clearly to be regarded as no more than a crude first approximation to the actual form of population growth. However, with the present set of data it is necessary, for estimation purposes to make some such an assumption for it is not possible to deduce from data of one single year whether the population size is increasing, decreasing or static. It is evident that a more refined analysis of population growth can be applied only to extensive acts of data obtained in several successive years.

ACKNOWLEDGMENTS

Masaharu Nishiwakis' " Age characteristics of Ear Plugs of Whales " reprinted from the *Scientific Reports of the Whales Research Institute*, No. 12, 1957 was received after completion of the foregoing account. It is gratifying to see that his results, based on a much smaller sample are in general agreement with the above. His new figure of 64 ft., for the age at sexual maturity of female Fin Whales does not coincide with previously published figures but if applied to Text-Fig. 3 of the present paper, it would give an age at sexual maturity of 4–5 years, which is identical with his own published result.

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APPENDIX

TABLE A.—*Female Antarctic Fin Whales* Balaenoptera physalus *Sample Area I*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1284	58	5	2½	58
863	63	6	3	32
1714	65	6	3	27
352	67	6	3	36
1820	68	6	3	25
2013	58	7	3½	58
1200	59	7	3½	59
1850	61	7	3½	30
739	63	7	3½	30
1785	64	7	3½	25
1819	68	7½	3¾	35
648	69	7	3½	37
601	69	7	3½	45
1707	58	8	4	58
652	58	8	4	58
776	60	8	4	25
1856	60	8	4	30
871	65	8	4	30
1454	66	8	4	26
2059	60	9	4½	—
1864	60	9	4½	33
1930	61	9	4½	31
2126	62	9	4½	27
1748	63	9	4½	24
1108	64	9	4½	48
933	65	9	4½	33
1118	65	9	4½	—
1248	67	9	4½	37
1036	68	9	4½	40
1813	68	9	4½	33
519	60	10	5	34
2043	60	10	5	23
1749	63	10	5	37
1898	63	10	5	35
1247	66	10	5	30
859	67	10	5	35
1279	69	10	5	34
1196	73	10	5	33
1937	62	11	5½	14
515	64	11	5½	—
1890	65	11	5½	40
1821	65	11	5½	62
1817	66	10	5	33
935	66	11	5½	30
1165	68	11	5½	46
1167	61	12	6	18
1208	63	12	6	34
448	67	12	6	44
1320	67	12	6	44
1034	67	12	6	35
1209	68	12	6	49
786	73	12	6	45
2095	76	12	6	40
1812	64	13	6½	—
2097	65	13	6½	—
670	72	13	6½	50
656	67	14	7	36
2128	67	14	7	40
1968	68	14	7	40
1784	68	14	7	35

TABLE A—cont.

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
906	70	14	7	34	529	70	26	13	53
1901	70	14	7	34	1625	70	27	13½	42
1079	72	14	7	—	1816	73	27	13½	73
1811	67	15	7½	40	1704	73	27	13½	91
660	71	15	7½	52	1040	68	28	14	78
855	72	15	7½	43	743	74	28	14	78
1285	70	16	8	53	1169	68	29	14½	94
1775	71	16	8	34	747	69	29	14½	42
2044	72	16	8	50	1966	73	30	15	70
703	72	16	8	60	1280	70	31	15½	75
1675	72	16	8	40	672	70	32	16	80
1927	72	16	8	40	1710	71	32	16	66
562	73	16	8	56	1630	74	32	16	87
1823	77	16	8	42	486	75	32	16	52
513	69	17	8½	37	2134	76	32	16	55
737	71	17	8½	60	1628	75	33	16½	60
1854	74	17	8½	32	1633	67	34	17	74
784	68	18	9	25	482	75	34	17	70
896	71	18	9	34	780	75	35	17½	63
2136	71	18	9	42	741	67	36	18	70
1085	73	18	9	49	712	72	36	18	67
1964	74	19	9½	47	1933	72	36	18	45
898	70	20	10	50	2007	72	36	18	65
597	70	20	10	40	593	73	36	18	63
2099	70	20	10	50	1669	75	36	18	33
674	72	20	10	51	1931	76	37	18½	50
1664	72	20	10	60	1670	73	39	19½	73
646	74	21	10½	63	1044	68	40	20	60
1083	70	22	11	34	2015	70	40	20	75
1779	71	22	11	38	937	72	40	20	60
2122	72	22	11	29	1706	72	40	20	94
714	71	22	11	70	488	73	40	20	90
1739	73	23	11½	72	2085	72	42	21	70
894	71	24	12	56	1042	74	42	21	92
1788	71	24	12	—	2130	69	43	21½	53
1892	72	24	12	—	438	72	45	22½	58
700	72	24	12	27	906	75	46	23	145
603	73	24	12	53	1634	72	50	25	73
1366	73	24	12	—	1425	81	50	25	39
434	78	24	12	80	1250	69	54	27	75
398	67	24	12	67	1357	77	54	27	96
595	71	25	12½	—	1703	69	55	27½	69
749	71	25	12½	59	1163	70	56	28	60
745	70	26	13	—	1938	72	56	28	71
2099	70	26	13	50	1352	72	56	28	56
867	72	26	13	17	2009	75	66	33	93
1358	74	26	13	74	706	75	70	35	88
478	77	26	13	85	358	73	80	40	120

TABLE B.—*Male Antarctic Fin Whales* Balaenoptera physalus *Sample Area I*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1278	55	3½	1¾	—	1827	66	15	7½	42
9423	58	4	2	20	1894	66	15	7½	27
2047	60	4	2	26	356	66	15	7½	43
1700	64	6	3	14	904	67	15	7½	50
2041	58	7	3½	27	650	63	16	8	36
560	58	7	3½	58	1824	65	16	8	60
925	68	8	4	24	394	65	16	8	70
1972	61	8	4	30	525	66	16	8	48
1818	61	9	4½	41	1886	67	16	8	53
1932	61	9	4½	31	1202	67	16	8	63
1110	62	9	4½	41	1116	67	16	8	35
400	63	9	4½	24	1783	68	16	8	45
440	64	9	4½	38	2053	68	16	8	55
1786	64	9	4½	34	1629	65	17	8½	60
1115	67	9	4½	25	1667	66	17	8½	55
1781	65	9	4½	31	1453	67	17	8½	35
1702	61	10	5	56	1327	67	17	8½	45
1857	63	10	5	25	476	69	17	8½	50
900	66	10	5	68	531	67	17	8½	50
947	66	10	5	32	1637	69	17	8½	50
1858	67	10	5	43	869	69	18	9	69
517	62	11	5½	43	654	66	19	9½	38
1772	63	11	5½	29	658	71	19	9½	57
1201	69	11	5½	—	521	65	20	10	26
1638	63	12	6	41	1038	66	20	10	62
564	64	12	6	38	1032	66	20	10	53
1598	65	12	6	30	902	53	20	10	53
941	66	12	6	45	1081	67	20	10	40
1000	68	12	6	30	523	68	21	10½	—
974	62	13	6½	60	1363	73	21	10½	40
1296	64	13	6½	47	490	66	22	11	46
1244	64	13	6½	40	1355	66	22	11	62
931	65	13	6½	37	857	68	22	11	60
2057	65	13	6½	42	939	71	22	11	54
1862	65	13	6½	37	1257	71	22	11	—
2045	67	13	6½	43	1671	67	40	20	50
1194	69	13	6½	38	1861	70	40	20	100
708	62	14	7	43	1356	66	42	21	77
1206	62	14	7	48	927	66	43	21½	78
558	65	14	7	48	976	68	43	21½	77
865	65	14	7	35	1326	65	43	21½	42
1243	66	14	7	27	1198	66	44	22	80
1742	66	14	7	55	1121	66	44	22	50
1203	67	14	7	30	716	68	45	22½	38
2005	67	14	7	13	1238	66	46	23	85
1663	68	14	7	42	1860	68	46	23	94
1205	64	15	7½	38	1825	67	49	24½	65

TABLE B—*cont.*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1112	64	50	25	65	1902	68	23	11½	—
1452	68	50	25	50	2049	71	23	11½	57
1745	71	50	25	85	1635	64	24	12	35
1776	65	52	26	52	480	67	24	12	58
1978	67	52	26	68	1071	68	24	12	55
710	65	53	26½	65	1451	70	24	12	40
568	62	54	27	88	1274	74	24	12	45
1077	66	54	27	46	363	63	25	12½	45
1113	68	54	27	58	1286	67	25	12½	43
605	66	55	27½	83	1251	70	25	12½	56
442	71	59	28½	63	1674	67	26	13	43
1636	63	56	28	62	1743	65	26	13	—
1627	65	59	28½	90	1822	79	26	13	45
406	65	56	28	62	945	64	27	13½	57
1741	65	58	29	67	2051	66	27	13½	53
1744	68	58	29	40	1599	63	28	14	63
396	67	59	29½	77	1111	67	28	14	62
662	66	60	30	85	1965	69	28	14	62
1073	72	60	30	120	1239	68	29	14½	82
1855	68	61	30½	65	704	70	29	14½	—
1705	73	62	31	80	772	65	30	15	65
1353	70	63	31½	50	1740	66	30	15	48
527	65	66	33	80	1888	66	30	15	83
702	70	67	33½	68	1815	69	30	15	47
1252	73	70	35	—	2083	65	31	15½	70
1120	65	71	35½	100	1207	68	31	15½	68
416	68	75	37½	—	2120	65	32	16	60
570	67	76	38	130	1423	70	33	16½	40
788	66	76	38	84	1666	66	35	17½	33
1075	64	85	42½	72	1893	64	36	18	58
676	64	83	41½	95	1450	69	36	18	80
1325	64	23	11½	42	1240	70	36	18	80
1777	65	23	11½	46	1597	71	36	18	40
2132	65	23	11½	40	361	65	37	18½	48
1774	67	23	11½	65	1626	67	38	19	60
2087	68	23	11½	33	1671	67	40	20	50

TABLE C.—*Female Antarctic Fin Whales* Balaenoptera physalus *Sample Area II*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Factory ship
1480	60	3	$1\frac{1}{2}$	20	Southern Venturer
A1493	62	5	$2\frac{1}{2}$	25	,, ,,
A1231	67	5	$2\frac{1}{2}$	30	Balaena
—	63	6	3	—	,,
—	61	7	$3\frac{1}{2}$	18	,,
1259	59	7	$3\frac{1}{2}$	28	,,
A1485	62	7	$3\frac{1}{2}$	30	Southern Venturer
1236	74	8	4	32	Balaena
—	65	9	$4\frac{1}{2}$	34	,,
1745A	65	9	$4\frac{1}{2}$	25	Southern Venturer
1239	66	9	$4\frac{1}{2}$	40	Balaena
A1261	67	10	5	40	,,
A1234	67	10	5	40	,,
—	68	16	8	35	,,
—	70	11	$5\frac{1}{2}$	—	,,
A1232	70	11	$5\frac{1}{2}$	40	,,
A1250	70	12	6	37	,,
A1550	70	12	6	—	Southern Venturer
1741	68	12	6	45	,, ,,
A1532	74	12	6	—	Balaena
A1255	71	12	6	—	,,
A1539	72	13	$6\frac{1}{2}$	40	,,
A1228	72	14	7	50	,,
A1233	72	15	$7\frac{1}{2}$	43	,,
—	68	16	8	95	,,
1251	76	18	9	50	,,
1253	76	19	$9\frac{1}{2}$	34	Southern Venturer
A1486	72	20	10	58	Southern Venturer
—	74	21	$10\frac{1}{2}$	55	Balaena
1252	75	21	$10\frac{1}{2}$	80	,,
A1494	72	21	$10\frac{1}{2}$	58	Southern Venturer
A1240	72	22	11	78	Balaena
1247	78	22	11	90	,,
A1490	75	24	12	—	Southern Venturer
1230	73	28	14	—	Balaena
A1348	77	29	$14\frac{1}{2}$	78	,,
A1547	75	30	15	65	,,
1478	73	31	$15\frac{1}{2}$	88	Southern Venturer
—	75	32	16	67	Balaena
A1235	75	32	16	85	,,
1747	73	32	16	55	Southern Venturer
A1242	73	33	$16\frac{1}{2}$	48	Balaena
—	75	34	17	100	,,
1742	68	38	19	85	Southern Venturer
—	72	42	21	105	Balaena
A1739	75	43	$21\frac{1}{2}$	64	Southern Venturer
A1536	78	44	22	60	,, ,,
A1538	77	46	23	60	Balaena
1243	74	47	$23\frac{1}{2}$	115	,,
A1748	76	48	24	64	Southern Venturer
A1740	74	50	25	87	,, ,,
A1547	75	30	15	65	Balaena
A1555	79	53	$26\frac{1}{2}$	75	,,
A1534	75	62	31	100	,,
—	78	66	33	83	,,

TABLE D.—*Male Antarctic Fin Whales* Balaenoptera physalus *Sample Area II*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Factory ship
A1487	55	5	$2\frac{1}{2}$	20	Southern Venturer
—	63	8	4	10	Balaena
1488	63	8	4	36	Southern Venturer
—	63	9	$4\frac{1}{2}$	35	Balaena
1497	63	9	$4\frac{1}{2}$	53	Southern Venturer
1416	65	9	$4\frac{1}{2}$	58	,, ,,
A1749	55	9	$4\frac{1}{2}$	30	,, ,,
A1492	63	10	5	53	,, ,,
1475	66	11	$5\frac{1}{2}$	30	,, ,,
—	65	14	7	—	Balaena
—	70	16	8	50	,,
1744	69	16	8	24	Southern Venturer
—	68	19	$8\frac{1}{2}$	84	Balaena
1484	71	19	$9\frac{1}{2}$	80	Southern Venturer
—	71	20	10	24	Balaena
—	71	20	10	62	,,
—	70	22	11	50	,,
—	69	23	$11\frac{1}{2}$	35	,,
1735	69	23	$11\frac{1}{2}$	53	Southern Venturer
1737	70	31	$15\frac{1}{2}$	35	,, ,,
1495	69	30	15	63	,, ,,
1489	72	32	16	50	,, ,,
—	68	34	17	47	Balaena
—	70	34	17	—	,,
—	70	36	18	30	,,
—	69	40	20	75	,,
—	70	40	20	43	,,
—	70	43	$21\frac{1}{2}$	40	,,
—	71	44	22	24	,,
1736	67	45	$22\frac{1}{2}$	95	Southern Venturer
A1488	67	50	25	36	,, ,,
1481	65	59	$28\frac{1}{2}$	55	,, ,,
A1738	76	63	$31\frac{1}{2}$	80	,, ,,

TABLE E.—*Unlogged Antarctic Fin Whales* Balaenoptera physalus

Males		Females	
Whale number	Estimated age (years)	Whale number	Estimated age (years)
1600	16	1168	4
1321	12	773	$4\frac{1}{2}$
1??5	$9\frac{1}{2}$	474	4
890	$32\frac{1}{2}$	757	$10\frac{1}{2}$
1715	$23\frac{1}{2}$	912	$4\frac{1}{2}$
1969	9	1164	13
—	10	1319	$1\frac{1}{2}$
—	$17\frac{1}{2}$	480	4
—	$11\frac{1}{2}$	—	9
—	$8\frac{1}{2}$	—	$18\frac{1}{2}$
—	19	—	9
—	12	—	11
—	$12\frac{1}{2}$	—	$9\frac{1}{2}$
—	$12\frac{1}{2}$	—	16
—	$12\frac{1}{2}$	—	6
—	$4\frac{1}{2}$	—	$6\frac{1}{2}$
—	4	—	8
—	—	—	$6\frac{1}{2}$
—	—	—	15
—	—	—	$7\frac{1}{2}$